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Advancing research on alien species and biological invasions

Alien plants tend to occur in species-poor communities

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Abstract

Invasive alien species can have severe negative impacts on natural ecosystems. These impacts may be particularly pronounced within ecological communities, where alien species can cause local extinctions. However, it is unclear whether individual alien plant species consistently occur in species-poor or species-rich communities across broad geographical scales and whether this pattern differs amongst habitat types. Using ~17,000 vegetation plots sampled across the Czech Republic, we calculated the median, range and skewness of the distribution in community species richness associated with 73 naturalised alien plant species. We compared the observed values with those obtained under a null expectation to test whether alien species occurred at random with respect to species richness in forest and grassland communities. We found that the relationship between the occurrence of alien species and the diversity of local plant communities was species-dependent and varied across habitats. Overall, however, alien species occurred in species-poor communities more often than expected by chance. These patterns were more pronounced in grasslands, where alien species also occurred in communities with a lower range of species richness than under random expectation. Our study represents one of the most comprehensive quantitative analyses relating alien plant invasion to resident community diversity at a broad geographical scale. This research also demonstrates that multi-species studies are needed to understand the processes of community assembly and to assess the impact of alien plant invasions on native diversity.

Keywords

biotic acceptance, biotic resistance, community ecology, Czech Republic, plant invasion, species richness

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Introduction

The spread of alien invasive species has serious environmental and socioeconomic impacts (Vitousek et al. 1997; Richardson and Pyšek 2008). These impacts are evident across spatial scales, but can be particularly pronounced within ecological communities, where invasive species can alter species composition and lead to local extinctions (Richardson and Pyšek 2006). Identifying the mechanisms of alien plant invasion in ecological communities is crucial for understanding the factors that support and constrain biodiversity and, ultimately, for designing effective management plans.

In recent decades, many ecologists have attempted to explain what makes native communities vulnerable to invasion (Lonsdale 1999; Chytrý et al. 2008) and whether communities hosting more species are more resistant to invasion than communities with fewer species (Elton 1958; Jeschke et al. 2018). According to the "biotic resistance hypothesis", communities with higher numbers of native species are more resistant to the establishment of incoming alien species than communities with lower numbers of native species (Elton 1958; Lonsdale 1999; Jeschke 2014). Consequently, this hypothesis predicts a negative correlation between native and alien species richness. This hypothesis is a special case of the "empty niche" hypothesis, which posits that naturalising species can occupy under-utilised niches and exploit available resources in communities unsaturated with native species (MacArthur 1970). However, empirical studies have also reported the opposite pattern, namely a positive correlation between native and alien species richness (Stohlgren et al. 1999; McKinney 2002), leading to the formulation of the "biotic acceptance hypothesis" (Stohlgren et al. 2003, 2006).

This "invasion paradox" can be partially resolved by considering the spatial scale at which biological invasions occur. Biotic resistance is thought to occur more frequently in relatively small areas where biotic interactions operate, whereas biotic acceptance is thought to become more important at larger spatial scales due to favourable environmental conditions and greater environmental heterogeneity (Levine 2000; Herben et al. 2004; Fridley et al. 2007). That is, if the environment is suitable for sustaining a high number of native species, it will also be suitable for the establishment of a high number of alien species (Naeem et al. 2000; Stohlgren et al. 2003). Nonetheless, alien species that successfully establish in species-rich communities can also reduce the diversity of recipient communities if they become dominant (Hejda et al. 2009, 2021), likely masking the net effects of biotic resistance and acceptance in observational studies. Examining the relationship between native community diversity and alien species abundance can inform us on how alien species impacts develop during the invasion process and help to design appropriate management strategies (Bradley et al. 2019).

The traditional niche theory also has difficulty explaining invasion patterns in species-rich communities because sites with high species richness generally do not provide as many niches to support such high plant diversity (Bell 2001). As an alternative, Hubbell (2001) proposed the neutral theory, which explains species coexistence within communities through stochastic processes, such as birth and death of individuals and colonisation and extinction of species. Many subsequent studies have

demonstrated that deterministic and stochastic (neutral) processes are not mutually exclusive and act simultaneously to drive invasion patterns in ecological communities (Daleo et al. 2009).

Although our understanding of alien species invasion patterns has advanced significantly in recent decades, questions remain about how alien species become established in ecological communities and impact community diversity. For example, several studies have examined the association between alien species and the average species richness in the invaded communities (e.g. Fridley et al. 2007; Hejda et al. 2009; Peng et al. 2019), but no studies have yet examined the association between alien species and the range and skewness of the distribution in species richness of the invaded communities (Fig. 1). If alien species tend to occur in communities with a similar number of species, that is, over a relatively low range of species richness or short richness gradient, then this may be interpreted as a sign of a narrow niche or habitat specialisation. Within a specific range of species richness, the distribution of alien species may be asymmetric. Some species may mainly occur in species-poor communities and only establish sporadically in species-rich communities (positive skewness). In contrast, other species may mostly occur close to the higher end of the species richness gradient and only establish sporadically in species-poor communities (negative skewness). The association between alien species and community richness may also be consistent within major plant clades, which would indicate that the ecological niches of alien species are phylogenetically conserved (Wiens and Graham 2005). Combining these different parameters, which collectively define the distribution of species rich-

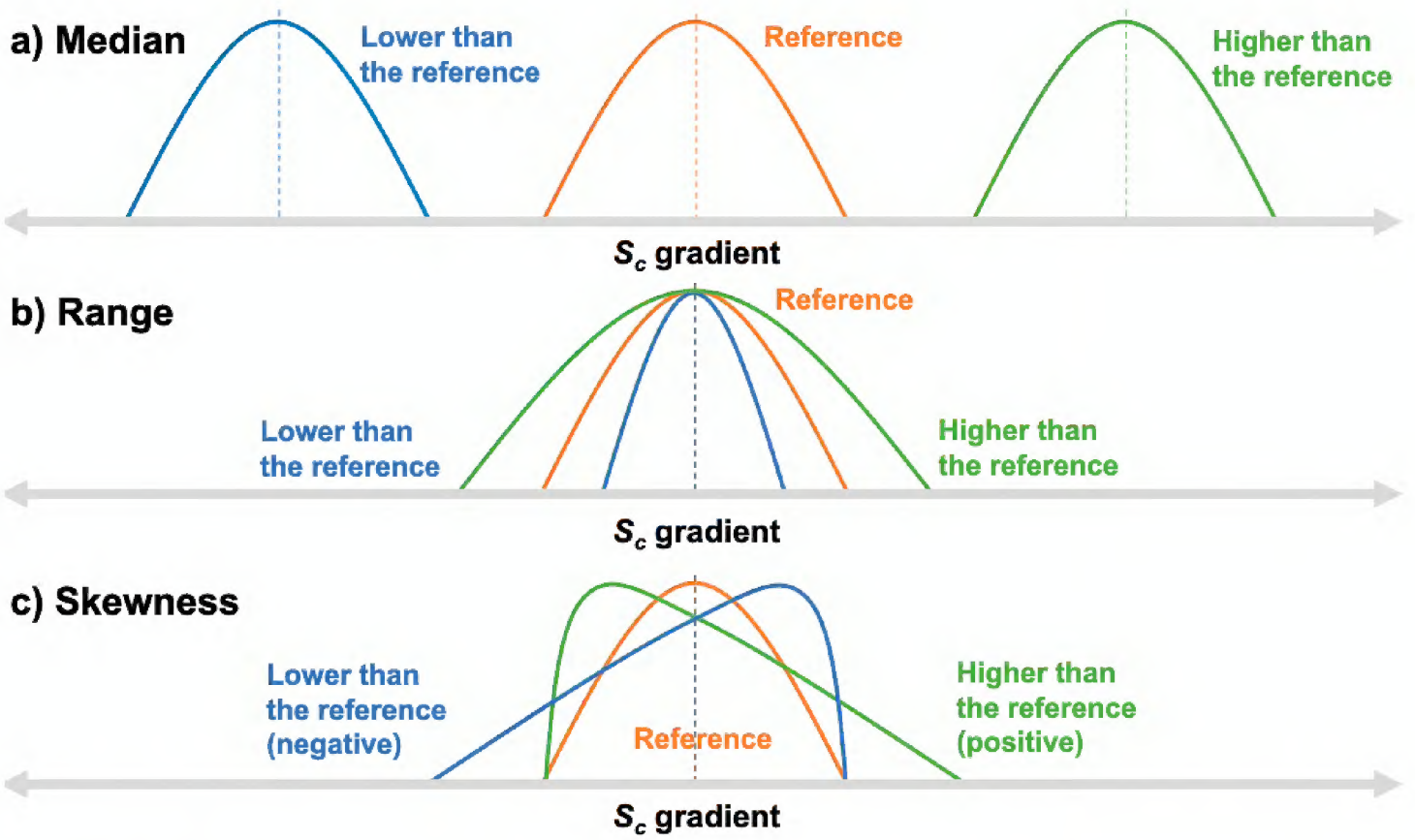

Figure 1. Schematic representation illustrating how the variation in the distribution of community species richness (S_c), associated with individual species is described by the (**a**) median, (**b**) range and (**c**) skewness.

ness associated with individual alien species, also across the tree of life, can give us insights into the ecology of alien species and improve our understanding of invasion processes.

Here, we aim to complement previous observational and empirical studies that have examined the association between the occurrence of alien species and species richness in terrestrial plant communities. We based our investigation on ~ 17,000 invaded and non-invaded vegetation plots sampled across the Czech Republic, which collectively hosted 73 naturalised alien species. Unlike previous studies, we calculated three main parameters for the tendency of individual species to occur: (1) in species-poor or species-rich communities, (2) in communities with a more or less variable number of species and (3) in communities with a symmetric or asymmetric distribution of species numbers (Fig. 1). We studied these three parameters using a null model approach to test whether the occurrence of alien species in forest and grassland communities differs from the random expectation. This knowledge can provide information for conservation plans to control the spread of aliens by targeting communities and habitats with the highest likelihood of hosting alien species.

We aim to answer two main research questions (RQs): (RQ1) Does the distribution of community species richness (median, range and skewness) associated with individual species differ between naturallzed alien and native species in forests and grasslands? (RQ2) Do naturalised alien species establish randomly in forest and grassland communities with respect to the species richness of these communities? Following the biotic resistance hypothesis, we expected that alien species would generally occur in communities with a smaller number of species than under the random expectation, regardless of the habitat in which they occur. We also expected that alien species associated with species-poor communities would generally occur in communities with a less diverse number of species and a positively skewed distribution in the number of species, indicating high specialisation of these species for stressed habitats. To complement RQ1 and RQ2 and help explain the main observed patterns, we additionally answer two secondary research questions: (RQ3) Are there consistent patterns in the relationship between community diversity and naturalised alien species amongst plant clades? (RQ4) Does the distribution of community species richness of individual naturalised alien species vary according to their level of dominance in the communities?

Methods

Vegetation data

We obtained vegetation-plot records from the Czech Republic from the Czech National Phytosociological Database (Chytrý and Rafajová 2003). Each vegetation plot in the database contains the percentage cover-abundance of all vascular plants present (in most cases derived from original data recorded using cover-abundance scales, such as the Braun-Blanquet scale). Taxon concepts and nomenclature follow the second edition of the Key to the Flora of the Czech Republic (Kaplan et al. 2019).

We assigned vegetation plots to phytosociological vegetation types (associations) following the classification system and the expert system for automatic classification

developed by Chytrý (2007–2013). We excluded plots that could not be unequivocally assigned to any association from this classification. To reduce differences in sampling intensity amongst areas and vegetation types, we stratified the database by phytosociological associations and geographically (within grid cells) and randomly selected a subset of plots in the strata that contained more plots than a specified threshold (see Chytrý 2007–2013 for details). This stratified resampling resulted in 30,115 plots covering all major vegetation types in the country. We removed plots from mires, wetlands and aquatic vegetation because these habitats reflect specific environmental conditions and had a low variation in species richness. We also removed plots of unknown size from this selection. The final dataset consisted of 16,987 plots, which we grouped into two major vegetation formations dominated by either trees and shrubs or herbaceous plants and dwarf shrubs (Suppl. material 1: Appendix S1). For simplicity, we refer to these vegetation formations as "Forests" (n = 4,492) and "Grasslands" (n = 12,495; this category also includes heathlands).

We excluded all taxa of bryophytes, lichens, algae and fungi, as well as the taxa identified at the genus level. We also aggregated subspecies at the species level and some commonly misidentified groups of related species into aggregates. We applied these filters to standardise the data and remove potential biases from multiple-source sampling (e.g. bryophytes and some subspecies were not recorded in all plots). The final dataset included 1,778 species of vascular plants.

Calculation of corrected species richness (S_c)

We computed the corrected species richness (S_c) for each plot to account for variable plot size in the database (Fibich et al. 2017). This calculation was done independently for each vegetation type (i.e. forests, scrub, alpine, grasslands, rocks, screes and walls and anthropogenic vegetation) by fitting a species-area relationship (Preston 1962):

$$S = cA^z \quad (1)$$

where S is species richness (i.e. the number of vascular plant species) in the plot, A is the plot area, z is the slope of the species-area relationship in log-log space and c is a constant that depends on the unit used for area measurement and equals the number of species that would occur in a unit-sized area. We then corrected species richness to the same plot size (A_m; the median plot size in each vegetation type; Suppl. material 1: Appendix S1):

$$S_c = S(A_m/A)^z \quad (2)$$

Classification of naturalized neophytes

We classified species as "naturalised neophytes" following the national catalogue of alien species (Pyšek et al. 2012). Naturalised taxa are alien plants that reproduce in the wild and sustain populations over many life cycles without direct or despite human

intervention. Neophytes are taxa occurring in the wild that humans have intentionally or unintentionally introduced to an area outside their native distribution range after the year 1500. In our classification, naturalised neophytes also included invasive neophytes. We repeated the analyses considering only "invasive neophytes" to test the robustness of our results. Invasive plants are naturalised alien plants that produce reproductive offspring, often in large numbers, at considerable distances from the parent plants, allowing them to spread over an extensive area (Richardson et al. 2000).

Statistical analyses

We performed all the analyses in R v. 4.1.0 (R Core Team 2021). To describe the distribution of community species richness associated with individual species, we assigned the S_c value of each plot to all species present in the plot. Then, we calculated the median, range and skewness S_c values of each species across all plots where it occurred (Fig. 1), separately in forests and grasslands. Finally, we calculated the mean of all median, range and skewness S_c values for all naturalised neophytes and all other species. To avoid the influence of rare species on our analyses, we did not calculate S_c values for species that occurred in fewer than five plots or fewer than 5% of plots in each vegetation formation.

The median S_c indicates the central position of the species on the species richness gradient (50^{th} percentile). The range indicates the spread or dispersion of S_c values around the median, while skewness indicates whether S_c values are asymmetrically distributed around the median. We calculated the standardised range as the Interquartile Range (IQR = 75^{th} percentile (Q3) – 25^{th} percentile (Q1)) divided by the square root of the median. We standardised the range by the square root of the median because the distribution of S_c approximates a Poisson distribution and, thus, the IQR depends on the mean and median. Without standardisation, the results for the range would be governed by this mathematical relationship. The range depends linearly on the standard deviation and the standard deviation is a square root of the mean in a Poisson distribution. As for the central distribution of species richness, we also used the median, which is approximately linearly dependent on the mean.

As a measure of skewness, we calculated the Pearson moment coefficient of skewness, which is the ratio of the third central moment to the cube of the standard deviation. We then standardised this metric by subtracting the expected skewness, based on a Poisson distribution ($1/\sqrt{\text{mean}}$). After this standardisation, positive values indicate greater and negative values smaller skewness than a Poisson distribution with the same mean. We used a parametric measure of skewness because we wanted to account for the effects of outliers and extreme values in our calculations and standardised non-parametric alternatives sensitive to these were not available. Correlations between the median and standardised range and skewness of S_c can be found in Suppl. material 1: Appendix S2.

We used Mann-Whitney U Tests to identify significant differences in the distribution of observed medians, ranges and skewness of S_c between naturalised neophytes and all other species in forests and grasslands (RQ1). This analysis is efficient in displaying

the distributions of the different richness parameters, but it retains the diversity gradients present in the vegetation. To remove the effects of these diversity gradients, we used a null model to test whether the mean of the median, range and skewness of S_c of naturalised neophytes differed from random expectation (RQ2). We randomised the community matrix (recoded as species presence/absence), maintaining species richness in plots and species frequency across all plots, thus without altering row and column totals. For randomisations, we used the "Curveball algorithm" (Strona et al. 2014), which can sample the set of all possible matrix configurations uniformly and requires much less computational effort than other methods, so that even large matrices can be randomised easily. Then, we recalculated the mean values of the median, range and skewness of S_c of each naturalised neophyte to obtain random S_c values for each parameter. We repeated this step 999 times to generate the null distribution of random means of the median, range and skewness of S_c. Finally, we compared the observed mean S_c of each parameter with the respective null distribution of random mean S_c and determined the *P*-values using the quantiles of the null distribution. We calculated *P*-values as the proportion of the random mean S_c that was lower than the observed mean S_c. *P*-values smaller than 0.025 indicated that the observed mean S_c of each parameter was significantly lower than expected by chance, whereas *P*-values larger than 0.975 indicated that the observed mean S_c of each parameter was significantly higher than expected by chance. We implemented the null model approach independently for each vegetation formation.

To examine whether the median, range and skewness of S_c of individual naturalised neophytes differed from the random expectation, we calculated the standardised effect sizes (SES) of these parameters as (observed parameter – mean of the expected parameter)/standard deviation of the expected parameter. For each parameter, SES < 1.96 indicates lower values than under random expectation, while SES > 1.96 indicates higher values than under random expectation. We plotted the SES of the different S_c parameters of the naturalised neophytes across the phylogeny to examine consistent patterns in ecological strategies amongst plant clades (RQ3). We created the phylogeny by linking our species to the mega-phylogeny implemented in the R package 'V.PhyloMaker' (Jin and Qian 2019). We used the 'scenario 3' approach in the same package to add missing species to the phylogeny (see more details in Jin and Qian 2019).

Finally, we examined whether the median S_c of individual neophytes varied according to their dominance in the communities (RQ4). Following Mariotte (2014), we classified species as dominant if they had relative cover ≥ 12% in each community. On the Braun-Blanquet scale, the 12% value separates species classified with the lowest degrees (i.e. r, +, 1 and 2m), which combine cover with abundance data, from those classified with the highest degrees, which are based on species cover alone. Therefore, species with relative cover ≥ 12% always have high cover and can be considered dominant in the community. We used Mann-Whitney U Tests to compare whether the distribution of median S_c differed when the species was dominant or non-dominant. We only considered species that occurred in at least ten plots in each group (i.e. dominant vs. non-dominant). We also repeated these analyses using a threshold of 25% in relative cover to test the effect of this choice on our results.

Data resources

The data underpinning the analysis reported in this paper are deposited in Zenodo at https://doi.org/10.5281/zenodo.6467402

Results

Comparing S_c of naturalised neophytes against all other species (RQ1)

We identified 25 and 60 naturalised neophytes in forests and grasslands, respectively. Compared with the other non-naturalised species, naturalised neophytes occurred more frequently in communities with fewer species in both forests (Fig. 2a) and grasslands (Fig. 2b). However, the ranges of richness values and their symmetry around the median did not differ between naturalised neophytes and all other species in either forests or grasslands. We found virtually identical results when we only considered invasive neophytes (Suppl. material 1: Appendix S3). The median and quantiles of S_c of each naturalised neophyte can be found in Suppl. material 1: Appendix S4.

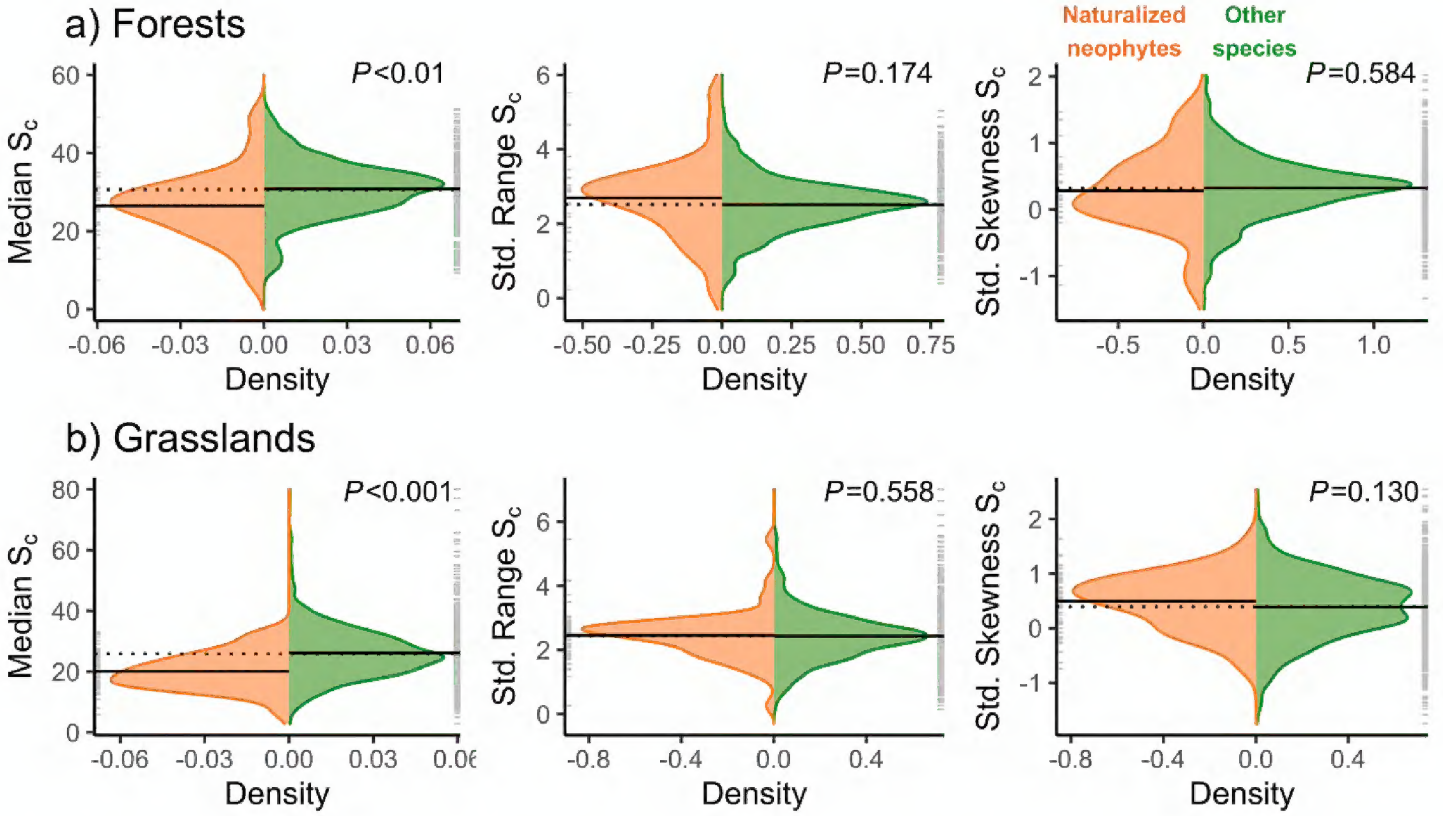

Figure 2. Density curves comparing the median (1st column), range (2nd column) and skewness (3rd column) of plot-size adjusted species richness (S_c) of naturalised neophytes with all other species in (**a**) forests and (**b**) grasslands. The dotted black line indicates the mean of S_c values for each parameter across all species in the vegetation formation. The solid black line indicates the mean of the S_c values for each parameter of each species group. The tick marks on the left and right margins show the S_c values for each parameter of individual species in each group. Density values of naturalised neophytes were multiplied by -1 to facilitate visual comparisons. The range and skewness of S_c were standardised (Std.) as described in the Methods section. *P*-values correspond to Mann-Whitney U Tests.

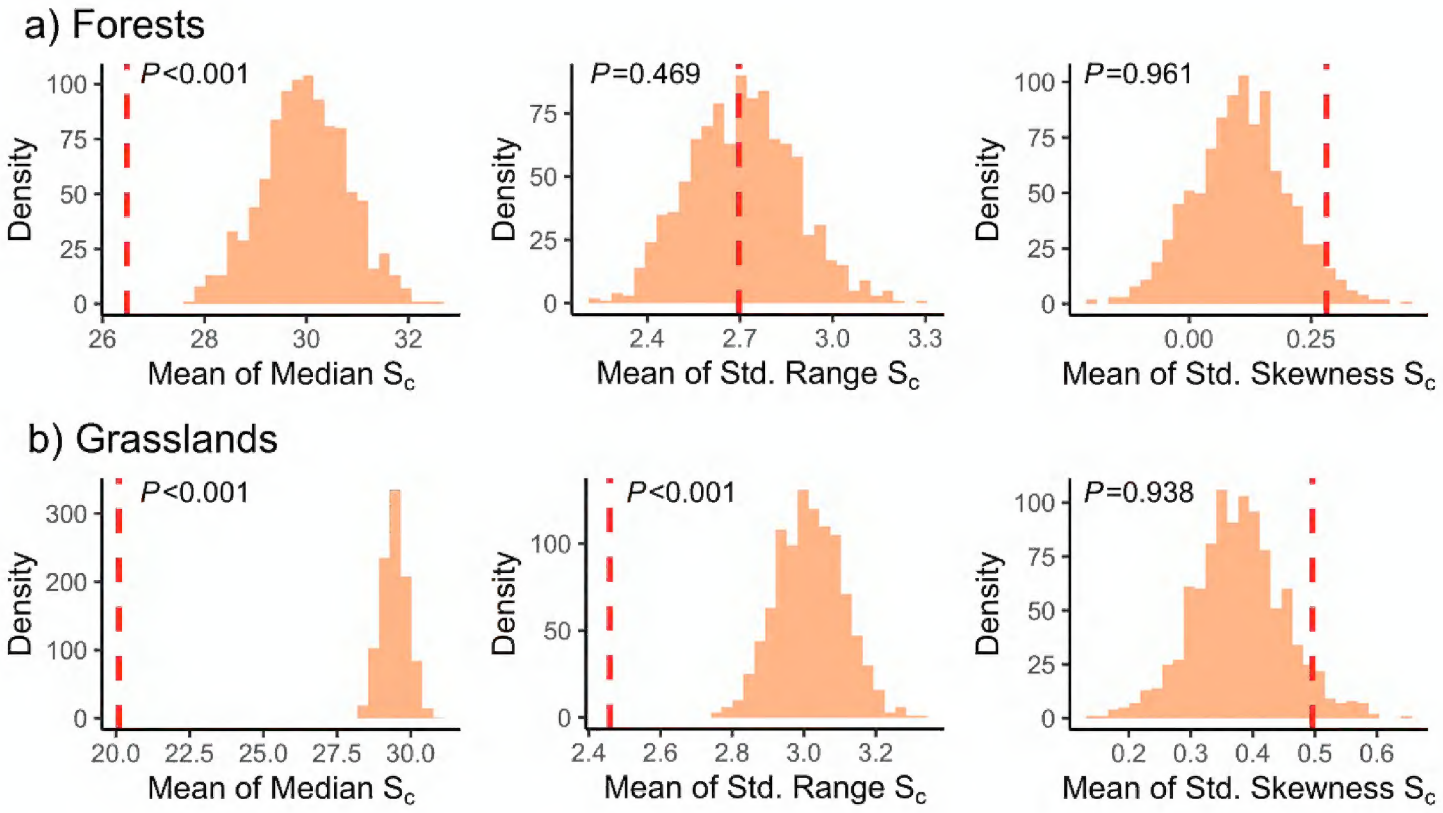

Figure 3. Comparison of mean observed values of the median (1st column), range (2nd column) and skewness (3rd column) of S_c of naturalized neophytes with the distribution of mean random values of the same parameters obtained from the null model. Results are for species in (**a**) forests and (**b**) grasslands. The dashed red line represents the mean observed value of each parameter across all species. The bars show the distribution of random values of each parameter. The range and skewness of S_c were standardised (Std.) as described in the Methods section. *P*-values indicate the proportion of the randomised parameters that are lower than the observed value.

Comparing S_c of naturalized neophytes against the random expectation (RQ2)

Naturalised neophytes tended to occur more frequently in communities with fewer species than expected by chance, both in forests (Fig. 3a) and grasslands (Fig. 3b). Naturalised neophytes also tended to occur in communities with a narrower range of richness values than under random expectation in grasslands. The symmetry in the distribution (skewness) of richness values of naturalised neophytes did not differ significantly from the random expectation.

Changes in S_c of naturalised neophytes amongst clades (RQ3)

Naturalised neophytes generally had lower than expected median S_c values (64%), particularly in grasslands (83%) (Fig. 4). Only *Reynoutria japonica* and *Aesculus hippocastanum* occurred in forest communities with more species than expected by chance. Fabaceae species generally did not deviate from the random expectation in terms of median S_c. Some clades also showed contrasting patterns between forests and grasslands. For example, the median S_c of naturalised neophytes from the Asteraceae family did not deviate from random in forests, but they showed lower median S_c than under random expectation in grass-

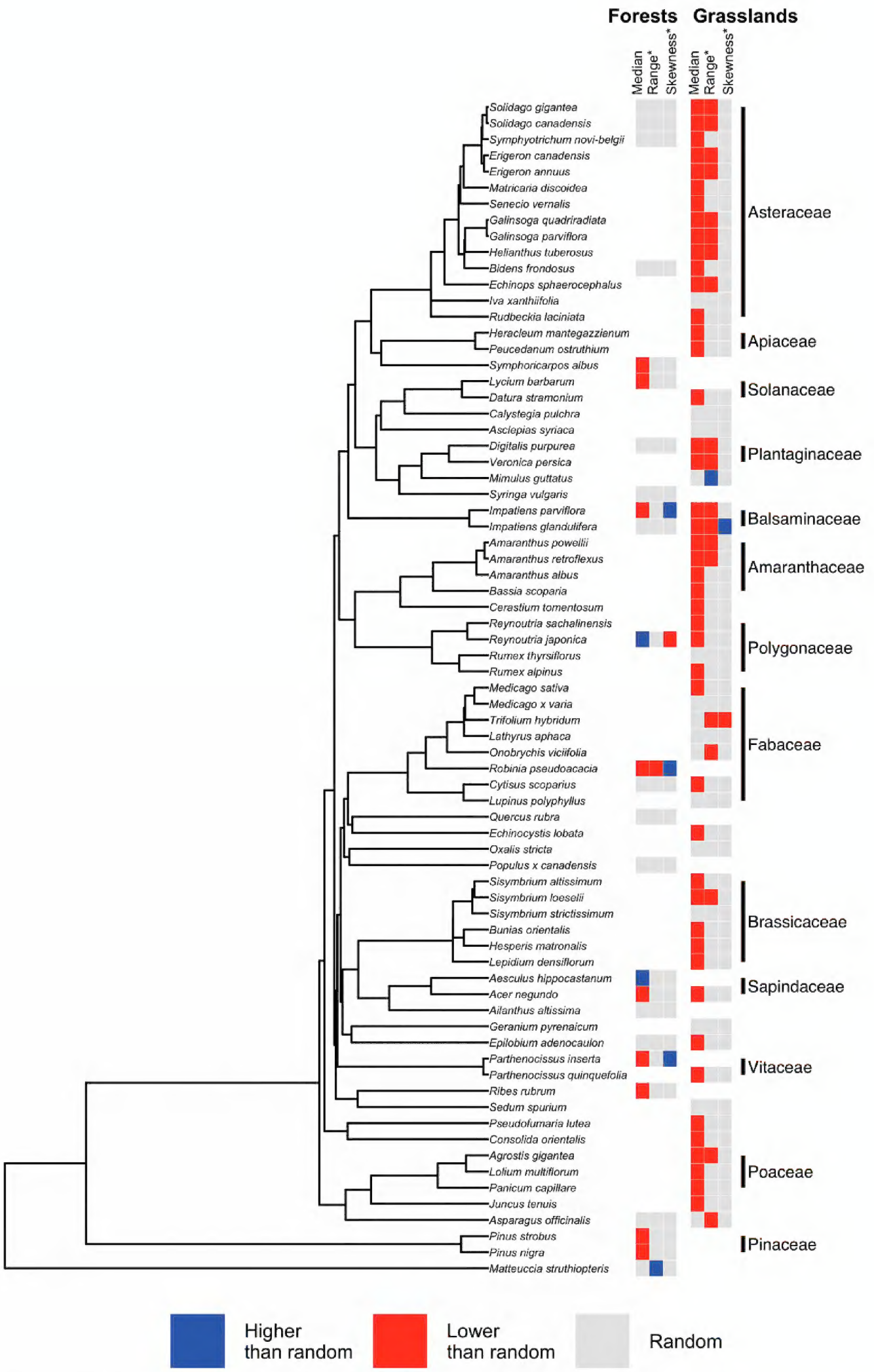

Figure 4. Phylogeny of naturalised neophytes found in vegetation plots. For each species, we show whether the median, range and skewness of S_c were higher (blue) or lower (red) than under random expectation or did not differ from the random expectation (grey) in forests and grasslands. The range and skewness of S_c were standardised as described in the Methods section. * = Standardised.

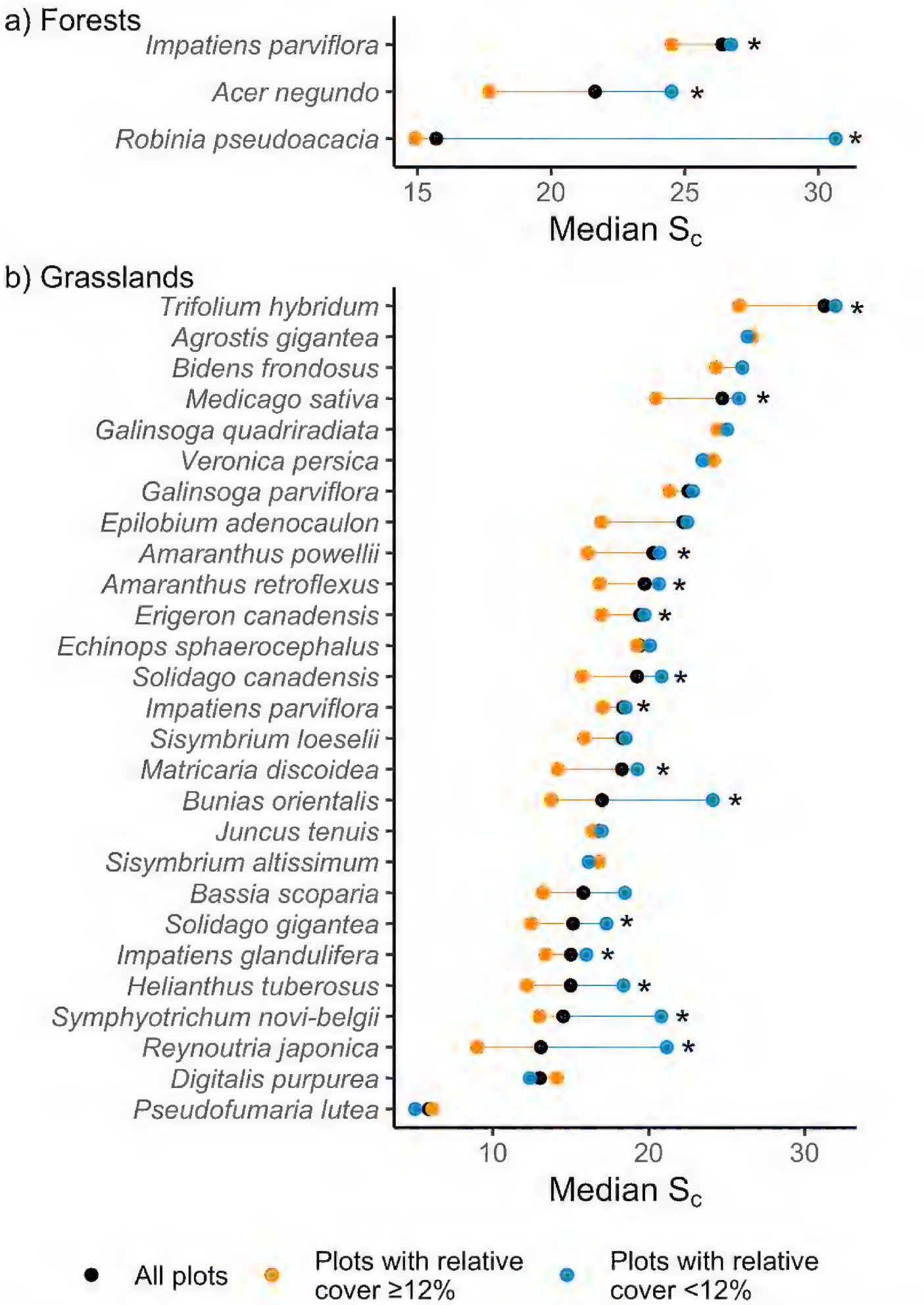

Figure 5. Median S_c of naturalised neophytes across all plots where they occurred and in plots with relative cover greater or smaller than 12%. Species are classified, based on their occurrence in (**a**) forests and (**b**) grasslands. Only species that occurred in at least ten plots in each group of plots (i.e. those with relative cover ≥ 12% vs. those with relative cover < 12%) were considered. Asterisks (*) indicate significant ($P < 0.05$) differences in median S_c between groups following Mann-Whitney U Tests. Median S_c values and number of plots associated with each species can be found in Suppl. material 1: Appendix S5: Table S5.2.

lands (see also *Digitalis purpurea*, *Impatiens glandulifera* or *Epilobium ciliatum*). About 31% of species in communities with a lower number of species than randomly expected also had a lower range of species richness than randomly expected. Only 7% of species that occurred in communities with a lower number of species than randomly expected were also more positively skewed towards species-poor communities than randomly expected.

Variation in S_c of naturalised neophytes with contrasting relative abundance (RQ4)

We found that naturalised neophytes generally had higher abundance (relative cover ≥ 12%) in communities with lower numbers of species than in communities with higher numbers of species in both forests and grasslands (Fig. 5). The most remarkable differences in median S_c of plots dominated (relative cover ≥ 12%) and not dominated (relative cover < 12%) by individual naturalised neophytes were for *Robinia pseudoacacia*, *Acer negundo* and *Reynoutria japonica*. Naturalized neophytes that frequently had low relative cover within communities (i.e. median S_c of all plots was similar to median S_c of plots with relative cover < 12%) included, for example, *Impatiens parviflora*, *Amaranthus retroflexus*, *Erigeron canadensis*, *Sisymbrium loeselii* and *Matricaria discoidea*. In contrast, naturalized neophytes that frequently had high relative cover within communities (i.e. median S_c of all plots was similar to median S_c of plots with relative cover ≥ 12%) included *Robinia pseudoacacia*, *Bunias orientalis* or *Symphyotrichum novi-belgii*. Although fewer naturalised neophytes reached a relative cover ≥ 25% in plots, we found similar results when we increased the cut-off for dominance to this value (Suppl. material 1: Appendix S5).

Discussion

Using a dataset spanning over a broad geographic area, we have demonstrated that the relationship between the occurrence of alien species and the diversity of local plant communities is species-dependent and varies by habitat. However, when considered together, alien species occur more frequently in species-poor communities than expected by chance. Alien species also occur in species-poorer communities than the rest of the flora in the Czech Republic. These patterns are more pronounced in grasslands, where alien species also occur in communities with a shorter diversity gradient (narrower range of richness) than would be expected by chance.

We suggest that the negative association between the occurrence of most alien species and community diversity in our study may be due to two main mechanisms. First, according to the biotic resistance hypothesis, diverse native communities might resist invasion by competition, herbivory and pathogens (Elton 1958; Lonsdale 1999; Jeschke 2014). Conversely, species-poor communities in stressed environments might have more empty niches available for alien species (MacArthur 1970). Second, alien species might initially establish in species-rich communities, but then cause local extinctions of resident native species, leading to a decline in overall diversity (Hejda et al. 2009).

It is likely that these two mechanisms act simultaneously to influence the association between alien species and community diversity. *Matricaria discoidea*, *Erigeron canadensis* and *Amaranthus retroflexus*, the three species associated with the lowest standardised median species richness in grasslands, grow primarily in species-poor ruderal vegetation, where they take advantage of gaps caused by various disturbance events to establish (Pyšek et al. 2009). Similarly, *Impatiens parviflora*, which was also associated with one of the lowest standardised median species richness in our study, invades most efficiently in disturbed forests with depauperated herb-layer communities, whereas more natural forests with species-rich herb layers appear to be more resistant to invasion by this neophyte (Obidziński and Symonides 2000). Previous studies have shown that invasive *Impatiens* species in the study area (*I. parviflora* and *I. glandulifera*) have only a minor impact on the native species diversity of invaded forests' herb layers (Hejda et al. 2009; Hejda 2012).

In contrast, some dominant invasive alien trees, such as *Robinia pseudoacacia* or *Pinus strobus*, inhibit understorey vegetation growth and native tree regeneration through a combination of effective seed dispersal, high seedling recruitment, fast growth or alteration of soil conditions (Hadincová et al. 2007; Cierjacks et al. 2013; Vítková et al. 2017). *Reynoutria japonica* is associated with species-poor communities in grasslands, but species-rich communities in forests. This difference can be partially explained by the fact that *R. japonica* more frequently invades riparian habitats, which are amongst the most species-rich forests in the study area, despite the potentially adverse effect of this species on community diversity (Hejda et al. 2021). However, *R. japonica* often becomes a strong dominant in herbaceous vegetation, overgrowing and out-competing other species (Hejda et al. 2009). Most herbaceous alien species from the Fabaceae family showed random associations with species diversity in grasslands. It is possible that these alien species do not occur in species-poor communities because they escape competition using nitrogen fixation through bacterial symbiosis and indirectly enrich the soil, allowing more species to become established (Sprent 2007). Nonetheless, most herbaceous legumes have also been actively sown, increasing the probability of their establishment regardless of the competition in the community. In general, alien species were associated with less species-rich communities when they exhibited high abundance, a pattern commonly observed in studies of native-invasive species interactions (Bradley et al. 2019).

We characterised individual naturalised alien species by calculating three key parameters (median, range and skewness) of the distribution of species richness of the communities in which the species occurred and compared these values to the null expectation to test if alien species assembled at random. As in previous studies, we confirmed that naturalised alien species generally occur in relatively species-poor communities (e.g. Fridley et al. 2007; Peng et al. 2019), but we also extend previous work by confirming that they can colonise species-poor communities with a narrower range in species number than expected by chance. This pattern was more evident in grasslands than in forests, indicating higher habitat specialisation of alien species in certain grassland types (Chytrý et al. 2008; Axmanová et al. 2021), perhaps reflecting the fact that our grasslands encompassed a broader range of vegetation types than forests. However, our species-level analyses showed that the associations of alien species with species-poor communities are not always accompanied by associations with a more

restricted range of species richness or greater asymmetry in their distribution. This coupling only occurred in two species (*Impatiens glandulifera* and *Robinia pseudoacacia*), which can be considered two highly specialised species that thrive under disturbance and eutrophic conditions in particularly species-poor sites. Further studies should also consider changes in beta-diversity at different levels of invasion to better characterise the relationships between alien species and community diversity and infer the impact of biological invasions on community structure. Such an approach will make it possible to examine whether individual alien species, belonging to particular clades, reduce community diversity and homogenise their composition when they become dominant.

To date, most studies examining native-alien species interactions had been conducted either at the plot level (e.g. Stohlgren et al. 2003, 2006; Boughton et al. 2011) or for a subset of alien species (e.g. Hadincová et al. 2007; Hejda et al. 2009, 2021), usually in a relatively small geographical area (Peng et al. 2019). A major strength of this study is that we calculated scores of individual species for their tendency to occur in species-poor or species-rich communities over a large area. Our analyses included invaded and non-invaded plots representing natural vegetation in the Czech Republic. Both invaded and non-invaded plots were combined in a null model approach to quantify the frequency, strength and consistency of non-random species associations. Although this approach assumes that all species in the regional species pool of each vegetation formation (i.e. forests and grasslands) can occur in plots of the same vegetation formation throughout the country, it allowed us to detect the signature of non-random mechanisms of community assembly and invasion. Our approach offers additional advantages over the methods used in the above studies when analysing large co-occurrence datasets and it could also be applied to other types of systems. For example, our approach could be used to test whether endemic or endangered species occur in species-rich or species-poor communities and ultimately provide information for conservation policy.

This study is one of the most comprehensive quantitative analyses to date examining the relationship between alien plants and the species richness of resident vegetation. The 73 alien species included in the study are considered invasive in most Central-European countries (Axmanová et al. 2021) and can be representative of plant invasions in the temperate zone. Europe has been a centre for international trade for many centuries, introducing many alien species to the continent (van Kleunen et al. 2018). This research also shows that multi-species studies are needed to understand the processes of community assembly and to assess the impact of alien plant invasions on native diversity. Supplementing our conclusions with results from long-term experimental community studies could provide further insights into the role of underlying factors driving biological invasions.

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Supplementary material 1

Alien plants tend to occur in species-poor communities

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Data type: Docx file.

Explanation note: **Appendix S1**: Overview of vegetation plots included in the different vegetation types. **Appendix S2**: Correlations between the median, range, and skewness of S_c. **Appendix S3**: Results for invasive neophytes. **Appendix S4**: The S_c statistics of individual naturalized neophytes. **Appendix S5**: Results considering a cut-off of 25% of cover to determine dominance.

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